

forest management

Group Clearfell Harvest Can Promote Regeneration of Aspen Forests Affected by Sudden Aspen Decline in Western Colorado

Wayne D. Shepperd, Frederick W. Smith, and Kristen A. Pelz

An experimental assessment of the use of clearfell harvesting to initiate a regeneration response in commercially managed aspen forests affected by sudden aspen decline (SAD) was conducted in western Colorado in cooperation with the USDA Forest Service. Nine pure commercial quality aspen stands, with three levels of mortality attributed to SAD, were selected (three replicates per mortality level). Half of each stand was clearfelled, and half was left uncut. The aspen regeneration response was monitored for three growing seasons after harvest in the cut and uncut treatments. Cut treatments with low and moderate mortality had the best subsequent regeneration response, and those with the heaviest mortality exhibited the poorest regeneration response. Uncut treatments exhibited very little regeneration response, regardless of the initial overstory mortality level. Dead trees in the uncut overstory were projected to fall within 15 years. These results indicate that it is possible to successfully regenerate aspen forests affected by SAD, provided that treatment occurs before the majority of the aspen are dead.

Keywords: *Populus tremuloides*, aspen regeneration, sudden aspen decline, coppice silviculture

Aspen (*Populus tremuloides* Michx.) is the most widely distributed tree species in North America (Shepperd et al. 2006), occurring from Alaska to New England and throughout mountainous areas of the West into Mexico. Since 2000, more than 3.2 million ha of aspen mortality have been mapped in North America (Worrall et al. 2013), including large areas in Ontario, Minnesota, Alberta, Saskatchewan, Utah, Arizona, and Colorado. Aspen is an important component of forest ecosystems in these areas and is economically important for recreation and commercial forest products. The observed mortality is uncharacteristic of these forests and has been a major concern to managers.

This rapid mortality, called sudden aspen decline (SAD) (Worrall et al. 2013), is characterized by rapid loss of the mature overstory with little or no subsequent aspen regeneration (Bartos and Shepperd 2010). SAD is thought to have been initiated by severe drought and high temperatures that occurred in the early 2000s (Worrall et al. 2013). These conditions triggered physiological water stress in affected trees, resulting in cavitation and hydraulic failure of conductive tissues in roots and branches that have been linked to sub-

sequent mortality (Anderegg et al. 2012). Mortality was exacerbated by biotic agents that attacked stressed trees, including *Cytospora* canker (usually caused by the fungus *Valsa sordida* Nitschke), aspen bark beetles (*Trypophloeus populi* Hopkins), poplar borer (*Saperda calcarata* Say), and bronze poplar borer (*Agilus liragus* Barter and Brown) (Worrall et al. 2008).

In Colorado, aerial surveys between 2003 and 2008 estimated that 220,000 ha (17% of the aspen cover type in the state) had aspen crown dieback and mortality (Worrall et al. 2010), which has been corroborated by local field observations. Site-specific data from the Mancos-Dolores Ranger District, San Juan National Forest showed a 3- to 5-fold increase in aspen stem mortality from 2003 to 2006 (Worrall et al. 2008). Many of these losses occurred in large pure commercial quality aspen forests.

The rapid mortality of mature trees associated with SAD differs from more slowly occurring mortality events that have also been called “aspen decline.” Generally, these slower declines are attributable to well-understood stresses on aspen vigor and are not unexpected. These stresses include those associated with old age, fire

Manuscript received June 4, 2014; accepted February 24, 2015; published online April 2, 2015.

Affiliations: Wayne D. Shepperd (Wayne.Shepperd@colostate.edu), USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO (retired). Frederick W. Smith (skip@warnernr.colostate.edu), Department of Forest and Range Stewardship, Colorado State University. Kristen A. Pelz (kristen.pelz@colostate.edu), Department of Forest and Range Stewardship, Colorado State University.

Acknowledgments: This research was made possible with a grant from the USDA Forest Service and generous contributions of time and effort by the staff of the Grand Mesa, Uncompahgre, and Gunnison National Forests and the Paonia Ranger District. We thank Dr. James Worrall and two anonymous reviewers for their helpful suggestions to improve the article.

This article uses metric units; the applicable conversion factors are: centimeters (cm): 1 cm = 0.39 in.; meters (m): 1 m = 3.3 ft; square meters (m²): 1 m² = 10.8 ft²; millimeters (mm): 1 mm = 0.039 in.; hectares (ha): 1 ha = 2.47 ac.

exclusion, competition with shade-tolerant conifers, or damage from extreme browsing pressure by large ungulates such as deer and elk (Romme et al. 1995, Kay 1997, Ripple and Larsen 2000, Bartos 2001, Kulakowski et al. 2004, Kaye et al. 2005, Smith and Smith 2005). In contrast, SAD events have been tied to acute drought stress (Anderegg et al. 2012) rather than factors that can be ameliorated with management activities. This mortality may be the precursor of future changes in the location and distribution of aspen due to climate change (Rehfeldt et al. 2009).

The general lack of new regeneration is a critical aspect of SAD. Healthy aspen typically regenerate by profuse root suckering after a disturbance that kills a tree. Although new research has conclusively shown that aspen seedlings do establish successfully and provide substantial genetic diversity to aspen forests throughout the western United States (Long and Mock 2012, Fairweather et al. 2014), managers must rely primarily on root suckers to provide the stem densities necessary to successfully regenerate commercial quality stands. Preharvest basal areas in such forests typically range between 30 and 60 m² ha⁻¹ and have about 2,500 regenerating stems ha⁻¹ in their understories (Crouch 1983). After past clearfell harvests, 1-year-old stem densities of <1,000,000 stems ha⁻¹ have been observed on some sites in Colorado (Shepperd 1993). Regeneration self-thins in a negative exponential pattern in the first years after establishment, but stands typically have densities exceeding 10,000 stems ha⁻¹ 10 years after cutting (Shepperd 1993).

Regeneration densities in SAD-affected stands are much lower than would be expected in healthy stands after overstory mortality due to fire or cutting. Worrall et al. (2008) found regeneration densities of ≤ 6,000 stems ha⁻¹ in all but one of their study locations with heavy mortality attributed to SAD. The reduced regeneration response is probably related to aspen root mortality associated with SAD (Worrall et al. 2010). SAD-affected plots had significantly lower length of live roots and greater length of dead roots than healthy plots (Worrall et al. 2010). Root mortality explained about 29% of the variation in crown loss (Worrall et al. 2010), hinting at the hydraulic root failure later verified experimentally by Anderegg et al. (2012). The apparent lack of a healthy root system in SAD-affected stands raises questions regarding their ability to successfully regenerate. Complete root system mortality in SAD-affected stands could result in entire aspen forests being permanently lost in a short amount of time. However, if these stands could be stimulated to regenerate before all overstory stems and the capacity of the root system to sprout is lost, it might be possible to establish new fully stocked aspen forests on SAD-affected sites.

In 2008, we initiated a research project in commercially managed SAD-affected forests in western Colorado to determine whether a clearfell-coppice removal of the remaining overstory trees could stimulate adequate levels of suckering to regenerate fully stocked aspen stands. We selected stands with varying levels of overstory mortality to evaluate the aspen regeneration response to harvesting. Our goals were to identify a threshold level of overstory mortality where SAD-affected commercially managed aspen stands could still be successfully regenerated and to provide guidance for managers during future climate-induced mortality events.

Methods

Study Area

The study area is located within the Terror Creek and Alder Creek watersheds of the Paonia Ranger District on the Grand Mesa, Uncompahgre, and Gunnison National Forests in southwestern

Colorado. This landscape is dominated by large-diameter commercial quality pure aspen stands (no conifer species present) that have experienced varying levels of SAD. These aspen forests are characteristic of the Colorado Plateau stable aspen type with predominate asexual regeneration and no dominant historic disturbance type or frequency (Rogers et al. 2014). Understory vegetation in the study area is dominated by serviceberry (*Amelanchier alnifolia* Nutt.) and snowberry (*Symphoricarpos oreophilus* A. Gray), typical of the *Populus tremuloides/Amelanchier alnifolia/Symphoricarpos oreophilus* community type (Alexander 1988). Average annual total precipitation in this landscape is between 660 and 737 mm year⁻¹. Average annual minimum temperature is between -3.2 and -2.3° C, and average annual maximum temperature is between 9.2 and 11.2° C (PRISM Climate Group 2012). Soils in this area are primarily Cryoborolls and Cryoboralfs derived from sedimentary substrate (US Department of Agriculture Soil Conservation Service 1975), and slopes are subject to mass movement. As a result, the topography is an irregular pattern of slopes and benches.

This area has a history of >30 years of successful aspen regeneration after clearfell harvesting of commercial forest products. The existence of numerous dense young stands in old cut blocks throughout these watersheds indicates that stand and site conditions were fully capable of regenerating new aspen forests before the occurrence of SAD. Although this landscape lies in an area projected by several climate models to lose aspen in the future (Rehfeldt et al. 2009), young stands in old cut blocks were not affected by SAD, similar to findings reported by Worrall et al. (2010).

Study Design

All pure aspen stands within a 1,500-ha area in the Terror Creek and Alder Creek watersheds were visually examined for signs of recent overstory mortality. A prism (basal area factor of 4.59 m² ha⁻¹) tally cruise of overstory trees (those >13 cm in diameter at 1.4 m dbh) was then performed in stands exhibiting mortality to determine the portion of basal area that had died. Cruised stands were stratified into three categories of overstory mortality based on the percentage of stand basal area that had died at the initiation of the study in 2008 (low, 0–20%; moderate, 20–60%; and high, >60%). We excluded stands that exhibited a regeneration response before the SAD outbreak (those containing >3,000 stems ha⁻¹ that were ≤13 cm at dbh). This allowed us to focus our efforts on determining whether nonregenerating aspen that were in decline could be stimulated to regenerate by removing the remaining overstory. Three spatially separate study sites (replicates) that contained stands in each mortality category were identified. Replicates 1 and 2 were on southerly aspects and replicate 3 was on a northeasterly aspect. All were between 2,680 and 2,840 m elevation.

Within each replicate, one aspen stand in each of the three mortality classes was chosen. Selected stands were a minimum of 4 ha, were located on similar topography and soils, and were accessible via an existing road system for commercial harvest. Selected stands were split, with half of each randomly selected for cutting, whereas the other half remained untreated. This allowed testing of the cut verses uncut treatment effect across the three crown dieback categories. Pairing cut and uncut treatments minimized site and genetic variation effects, as variation in those factors was assumed to remain constant within a selected stand. Stands were assumed to contain a majority of a single aspen genotype, as identified by phenotypic characteristics. Although it is likely that multiple genotypes were present (Long and Mock 2012), we assumed that all were capable of

a regeneration response. After cut treatments were randomly assigned, a monitoring area of ≥ 2 ha was delineated in adjoining cut and uncut portions of each stand to minimize the influence of topographic variability on treatment response. A minimum 60 m sampling buffer was observed between cut and uncut monitoring areas to minimize cross-treatment effects.

Pretreatment Data Collection

A minimum of five variable radius overstory inventory plots were established in each stand before cutting using a basal area factor of $4.59 \text{ m}^2 \text{ ha}^{-1}$ (yielding an average of 4–10 trees/plot). Plots were established by randomly locating an initial point near the edge of a monitoring area, with the remaining points placed in a systematic manner on compass bearings at tape-measured distances 30–60 m apart to ensure complete coverage of the monitoring area. All plots were permanently staked, and their positions were recorded. For each “in” tree (>13 cm dbh), we recorded species, status (live, dead, or declining), dbh, height, % recent crown loss, and presence/absence of damaging agents (e.g., wounds, broken stems, and canker diseases). For dead trees, the estimated time since death (≤ 2 years [bark intact] or >2 years [no bark]) was recorded.

Aspen regeneration was measured using 13.5 m^2 (2.07 m radius) plots located at the center of each variable radius plot to sample trees ≤ 13 cm dbh. Trees in these plots were tallied by status, size class, and occurrence of damage that appeared to be affecting tree vigor. Additional 13.5 m^2 regeneration plots were established midway between each pretreatment overstory plot.

Cut Treatment

The study was conducted as an Applied Silvicultural Assessment under the Healthy Forests Restoration Act. Cut treatment units were clearfelled under a commercial timber sale contract administered by the Grand Mesa, Uncompahgre, and Gunnison National Forests. All units were winter logged using tracked feller-bunchers and rubber-tire grapple skidders to cut and move trees to landings. The over-snow logging left no evidence of skid trails or soil disturbance in any units. Although all treatment units were originally scheduled to be harvested in the same year, 2 years were required to complete the timber sale contract because of operational and economic conditions. Replicate 1 was harvested during the winter of 2008–2009, and replicates 2 and 3 were harvested during the winter of 2009–2010.

Posttreatment Field Data

All plots were resampled after the first full growing season after harvest and annually through 2012. In the cut treatments, only fixed-radius regeneration plots were remeasured. In the uncut treatments, both overstory and regeneration plots were remeasured annually. The height of the tallest live stem on each regeneration plot was also recorded in 2012.

Data Analysis

All data were scaled to per ha values and summarized to the treatment unit level. SAS/STAT software (SAS Institute, Inc., Cary, NC) was used for all summaries and analyses. To test for treatment effects on regeneration density, we used a linear mixed-effects model with a random effect for plots to account for the repeated measures and a group effect for replicates. Aspen regeneration density was the dependent variable, and mortality level, cut treatment, year of measurement, the interaction of cut treatment and mortality level, and

Table 1. Results of the linear mixed-effects models testing for the effects of predictor variables on regeneration density (in 2010, 2011, and 2012) and the maximum regeneration height (in 2012).

Response	Predictor	<i>F</i>	<i>P</i>
Regeneration density	Mortality level	26.8	<0.001
	Cut treatment	260.8	<0.001
	Year	42.3	<0.001
	Mortality level \times cut treatment	34.0	<0.001
	Mortality level \times cut treatment \times year	8.7	<0.001
Maximum regeneration height	Mortality level	2.4	0.098
	Cut treatment	30.6	<0.001
	Mortality level \times cut treatment	16.3	<0.001

Both models included a group effect for replicates. The model for regeneration included a random effect for plots to account for repeated measures.

the interaction among the three were independent class variables (Table 1). We performed pairwise comparisons between all combinations of the mortality levels and cut treatment groups within years. We report significant differences at the $\alpha = 0.05$ level with a Tukey adjustment for the multiple comparisons within years.

To test for the effect of mortality level and cutting on the size of regeneration, we used a linear mixed-effects model with a group effect for replicates. Maximum regeneration height in 2012 was the dependent variable and mortality level, cut treatment, and the interaction among the two were independent class variables (Table 1). We performed pairwise comparisons between all combinations of the mortality levels and cut treatment groups. We report significant differences at the $\alpha = 0.05$ level with a Tukey adjustment for multiple comparisons.

Results

Treatment Response

There were striking differences in average regeneration (stems ≤ 13 cm dbh) densities between the uncut control units and the cut treatment units in the low- and moderate-mortality stands in all years (Figure 1). Cut unit regeneration densities were <10 times greater than uncut densities in the low-mortality stands ($P < 0.001$ in 2010, 2011, and 2012), and cut densities were >6 times greater than uncut densities in moderate-mortality stands ($P < 0.001$ in 2010, 2011, and 2012). High-mortality stands had significantly more regeneration in cut than in uncut units in 2010 ($P = 0.040$), but in 2011 and 2012 uncut and cut densities were not statistically different ($P = 0.085$ and $P = 0.199$, respectively). Regeneration density in cut treatments was significantly different among all three mortality levels in all years ($P \leq 0.042$ for all comparisons). Cut unit regeneration densities showed a trend of decline with time since treatment as would be expected in healthy self-thinning populations. Regeneration densities in the uncut treatments did not vary significantly among overstory mortality levels in any year ($P \geq 0.993$ for all comparisons) (Figure 1). Across all treatments, 80% of regenerating stems remained undamaged in 2012, the last year of observation. We compared average 2012 regeneration density in cut units with the average live overstory basal area present in those units immediately before cutting and found them to be linearly related (Figure 2).

Regeneration Height

In low- and moderate-mortality stands, the cut units had significantly taller regeneration than the uncut units in 2012 ($P < 0.001$ for low-mortality stands and $P = 0.003$ for moderate-mortality

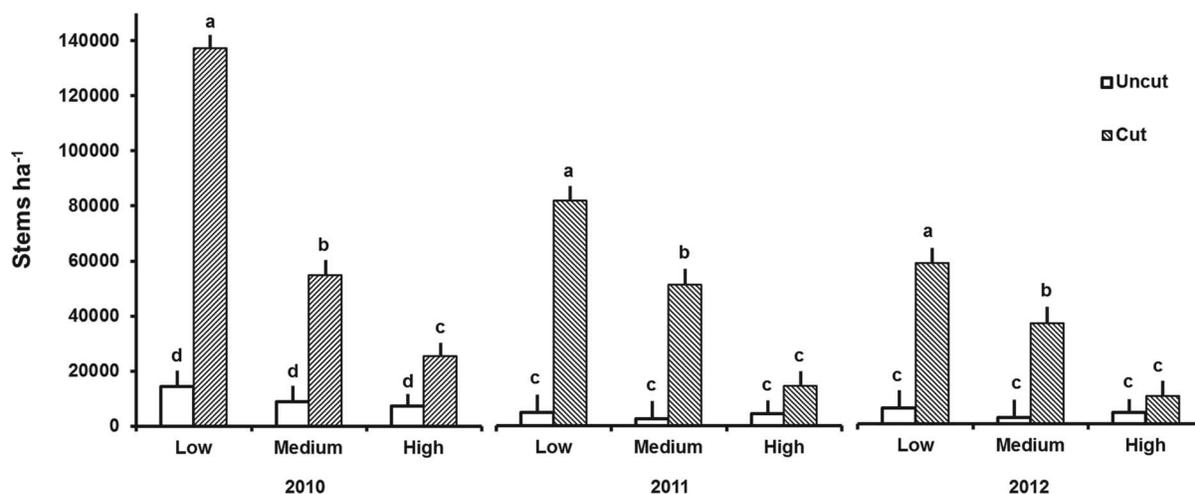


Figure 1. Average aspen regeneration live stem density per ha by year, treatment, and overstory mortality class, with SE bars. Bars with common labels within years are not statistically different, according to pairwise comparisons of means ($\alpha = 0.05$ with a Tukey adjustment for multiple comparisons within years).

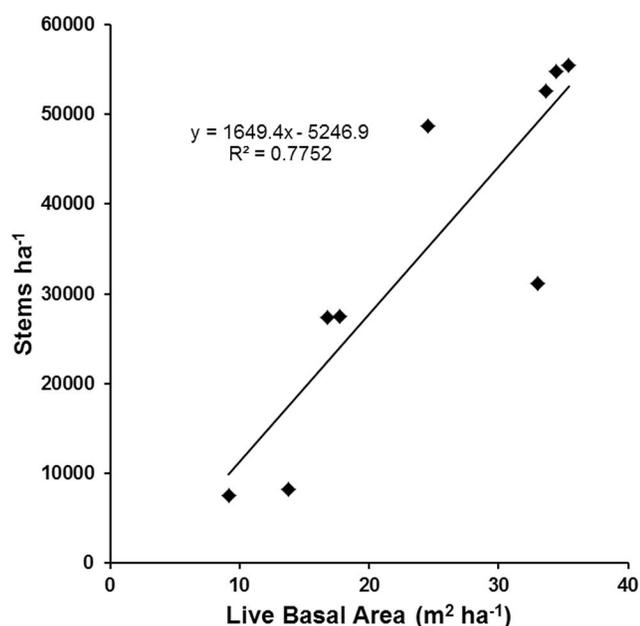


Figure 2. Relationship between live basal area existing immediately before harvest and 2012 regeneration density for the nine harvested units in the study.

stands) (Figure 3). In contrast, cutting had no effect on maximum regeneration height in the high-mortality stands ($P = 0.896$), where regeneration in both cut and uncut areas was taller than regeneration in uncut areas of low- and moderate-mortality stands ($P \leq 0.034$ for all comparisons) (Figure 3).

Tree Fall Progression

Live tree basal area in the uncut portions of the stands continued to decline (and dead basal area increase) over time in all mortality categories. Recently dead trees lost their bark and fell down during the observation period. This progression was apparent at all levels of mortality and prompted us to examine our individual overstory sample tree data to see whether we could estimate snag persistence. One-third of the 150 dead sample trees recorded during the course of this study had fallen by 2012. We noted a strong linear relation-

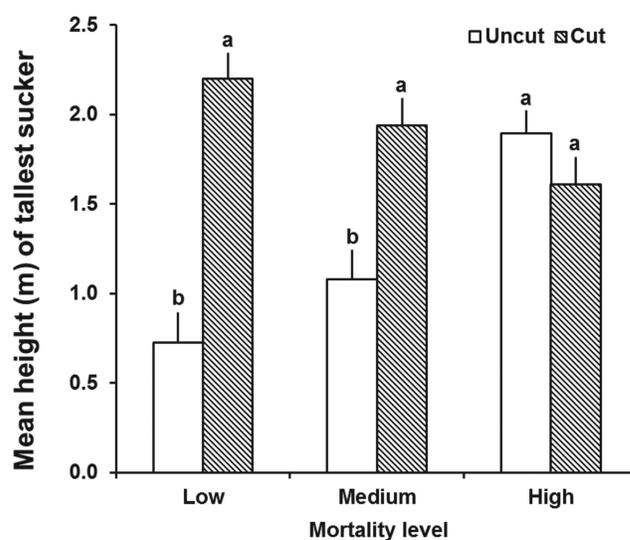


Figure 3. Average height of the tallest regeneration stem on plots in 2012 by treatment and overstory mortality level. Bars with common labels are not statistically different according to pairwise comparisons of means ($\alpha = 0.05$ with a Tukey adjustment for multiple comparisons).

ship between the percentage of standing snags and number of years since death (either known or estimated using criteria described earlier) (Figure 4). Projecting this relationship forward in time indicates that none of these snags are likely to remain standing 16–17 years after death (Figure 4).

Discussion

Commercial quality aspen forests affected by SAD similar to those in this study might be successfully regenerated by clearfell harvesting of overstory trees, provided that such harvest is implemented before complete overstory mortality occurs. The best post-harvest regeneration response in this study occurred in stands with low and moderate overstory mortality containing at least 15 m² ha⁻¹ live overstory basal area before harvest (Figure 2). Cut treatment regeneration densities in 2012 averaged 54,000 stems ha⁻¹ in low-mortality stands and 34,000 stems ha⁻¹ in moderate-mortality

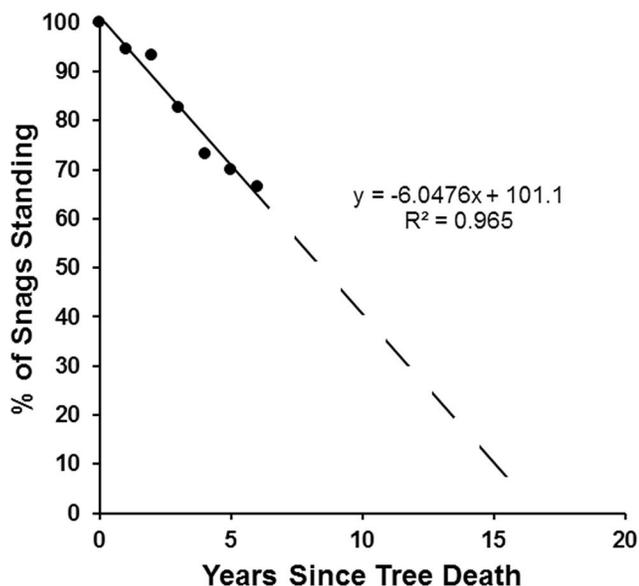


Figure 4. Estimate of snag longevity projected from the percentage of fallen dead trees observed in this study and the number of years since tree death.

stands. Although lower than the 200,000 stems ha^{-1} previously observed in dense 2-year-old regeneration (Shepperd 1993), they are comparable to densities of 55,000 stems ha^{-1} reported by Crouch (1983) for 3-year-old aspen regeneration in southwestern Colorado. The tallest regeneration was above the 2-m threshold needed to be out of reach of browsing domestic livestock (Shepperd et al. 2006), and <20% of stems were damaged.

We therefore expect these stands to develop into fully stocked commercial quality stands. Similar aspen forests units with low to moderate overstory mortality at the time of harvest could be expected to produce regeneration densities capable of growing into fully stocked commercial stands. However, recovery to pre-SAD stocking levels is uncertain in both uncut and cut high-mortality stands because of the lower regeneration response and the unknown effects of future self-thinning of regeneration in these low-density stands.

Dead trees continued to fall throughout the course of our study. We were surprised that our estimate of snag longevity was much less than previous estimates for aspen of 20–25 years (Lee 1998) and 40–50 years (Vanderwel et al. 2006). This rapid snag fall could be associated with increased root mortality in these SAD-affected stands. If so, there may be repercussions for long-term snag availability to cavity nesters and as perches for birds of prey and restricted access for large animals in other SAD-affected forests. It also means that heavy surface fuels will accumulate faster in these forests as the dead trees fall.

Management Implications

Although climate change may affect the future persistence of aspen in Colorado (Rehfeldt et al. 2009), our experience demonstrates that it may be possible for managers to successfully regenerate aspen forests affected by future aspen decline events. However, clearfelling did not increase regeneration in our study where the majority of the original stand basal area died before harvest. This finding suggests that managers will have to react quickly to respond to future decline events before too much mortality has occurred.

This project took 2 years from the initial design until harvest completion. This exceptionally short timeline was only possible because of streamlined procedures of the Applied Silvicultural Assessment under the Healthy Forests Restoration Act. We were also fortunate to have found an area of commercially managed aspen where SAD had not yet peaked and to have excellent support from Grand Mesa, Uncompahgre, and Gunnison National Forest staff in quickly planning and executing a commercial timber sale contract. A similar implementation timeline may not be realistic to reactively manage the next SAD event at the operational scales needed to be effective. Proactive management that diversifies landscape-scale age class structure by introducing vigorous new populations of aspen in areas that have been lightly affected by recent SAD, and/or areas that are projected to be unsuitable future habitat may help these forests be resilient to climate change and enable aspen persistence into the future (Worrall et al. 2013). Although this is potentially a daunting task, now is the time to begin, before the next SAD event occurs.

Literature Cited

- ANDEREGG, W.R., J.A. BERRY, D. DUNCAN, J.S. SMITH, L.D. SPERRY, L. ANDEREGG, AND C.B. FIELD. 2012. The roles of hydraulic and carbon stress in a widespread climate-induced forest die-off. *Proc. Natl. Acad. Sci. USA* 109(1):233–237.
- ALEXANDER, R.R. 1988. *Forest vegetation on national forests in the Rocky Mountain and Intermountain regions: Habitat types and community types*. USDA For. Serv., Gen. Tech. Rep. RM-162, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO. 47 p.
- BARTOS, D.L. 2001. Landscape dynamics of aspen and conifer forest. P. 5–14 in *Proc. of the Symposium on sustaining aspen in western landscapes, 13–15 June 2000, Grand Junction, CO*, Shepperd, W.D., D. Binkley, D.L. Bartos, T.J. Stohlgren, and L.G. Eskew (eds.). USDA For. Serv., Proc. RMRS-P-18, Rocky Mountain Research Station, Ogden, UT. 460 p.
- BARTOS, D.L., AND W.D. SHEPPERD (COMPS.). 2010. *The aspen mortality summit; December 18 and 19, 2006, Salt Lake City, UT*. USDA For. Serv., Proc. RMRS-P-60WWW, Rocky Mountain Research Station, Ogden, UT. 21 p. Available online at www.fs.fed.us/rm/pubs/rmrs_p060.pdf; last accessed June 1, 2014.
- CROUCH, G.L. 1983. Aspen regeneration after commercial clearcutting in southwestern Colorado. *J. For.* 83:316–319.
- FAIRWEATHER, M.L., E.A. ROKALA, AND K.E. MOCK. 2014. Aspen seedling establishment and growth after wildfire in central Arizona: An instructive case history. *For. Sci.* 60(4):703–712.
- KAY, C.E. 1997. Is aspen doomed? *J. For.* 95:4–11.
- KAYE, M.W., D. BINKLEY, AND T.J. STOHLGREN. 2005. Effects of conifers and elk browsing on quaking aspen forest in the central Rocky Mountains, USA. *Ecol. Applic.* 15(4):1284–1295.
- KULAKOWSKI, D., T.T. VEBLEN, AND S. DRINKWATER. 2004. The persistence of quaking aspen (*Populus tremuloides* Michx.) in the Grand Mesa area Colorado. *Ecol. Applic.* 14(5):1603–1614.
- LEE, P. 1998. Dynamics of snags in aspen-dominated midboreal forests. *For. Ecol. Manage.* 105(1–3):263–272.
- LONG, J.N., AND K. MOCK. 2012. Changing perspectives on regeneration ecology and genetic diversity in western quaking aspen: Implications for silviculture. *Can. J. For. Res.* 42(12):2011–2021.
- PRISM CLIMATE GROUP. 2012. *United States average annual precipitation, 1981–2010*. Oregon State University, Corvallis, OR. Available online at www.prism.oregonstate.edu/normals/; last accessed Oct. 28, 2014.
- REHFELDT, G.E., D.E. FERGUSON, AND N.L. CROOKSTON. 2009. Aspen, climate, and sudden decline in western USA. *For. Ecol. Manage.* 258(11):2353–2364.

- RIPPLE, W.J., AND E.J. LARSEN. 2000. Historic aspen recruitment, elk, and wolves in northern Yellowstone National Park USA. *Biol. Conser.* 95(3):361–370.
- ROGERS, P.C., S.M. LANDHAUSSER, B.D. PINNO, AND R.J. RYEL. 2014. A functional framework for improved management of western North American aspen (*Populus tremuloides* Michx.) *For. Sci.* 60(2): 345–359.
- ROMME, W.H., M.G. TURNER, L.L. WALLACE, AND J.S. WALKER. 1995. Aspen, elk, and fire in Northern Yellowstone National Park. *Ecology* 76(7):2097–2106.
- SHEPPERD, W.D. 1993. *Initial growth, development, and clonal dynamics of regenerated aspen in the Rocky Mountains*. USDA For. Serv., Res. Pap. RM 312, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO. 8 p.
- SHEPPERD, W.D., P.C. ROGERS, D. BURTON, AND D.L. BARTOS. 2006. *Ecology, biodiversity, management, and restoration of aspen in the Sierra Nevada*. USDA For. Serv., Gen. Tech. Rep. RMRS-GTR-178, Rocky Mountain Research Station, Fort Collins, CO. 122 p.
- SMITH, A.E., AND F.W. SMITH. 2005. Twenty-year change in aspen dominance in pure aspen and mixed aspen/conifer stands on the Uncompahgre Plateau, Colorado, USA. *For. Ecol. Manage.* 213(1): 338–348.
- US DEPARTMENT OF AGRICULTURE SOIL CONSERVATION SERVICE. 1975. *Soil taxonomy: A basic system of classification for making and interpreting soil surveys*. USDA, Agri. Handbk. 436, Washington, DC. 754 p.
- VANDERWEL, M.C., J.P. CASPERSEN, AND M.E. WOODS. 2006. Snag dynamics in partially harvested and unmanaged northern hardwood forests. *Can. J. For. Res.* 36(11):2769–2779.
- WORRALL, J.J., G.E. REHFELDT, A. HAMANN, E.H. HOGG, S.B. MARCHETTI, M. MICHAELIAN, AND L.K. GRAY. 2013. Recent declines of *Populus tremuloides* in North America linked to climate. *For. Ecol. Manage.* 299:35–51.
- WORRALL, J.J., L. EGELAND, T. EAGER, R.A. MASK, E.W. JOHNSON, P.A. KEMP, AND W.D. SHEPPERD. 2008. Rapid mortality of *Populus tremuloides* in southwestern Colorado, USA. *For. Ecol. Manage.* 255(3–4):686–696.
- WORRALL, J.J., S.B. MARCHETTI, L. EGELAND, R.A. MASK, T. EAGER, AND B. HOWELL. 2010. Effects and etiology of sudden aspen decline in southwestern Colorado, USA. *For. Ecol. Manage.* 260(5):638–648.